

# PALAEOENVIRONMENTAL DISTRIBUTION OF PROTEROZOIC MICROFOSSILS, WITH AN EXAMPLE FROM THE AGU BAY FORMATION, BAFFIN ISLAND

by NICHOLAS J. BUTTERFIELD *and* FREDERICK W. CHANDLER

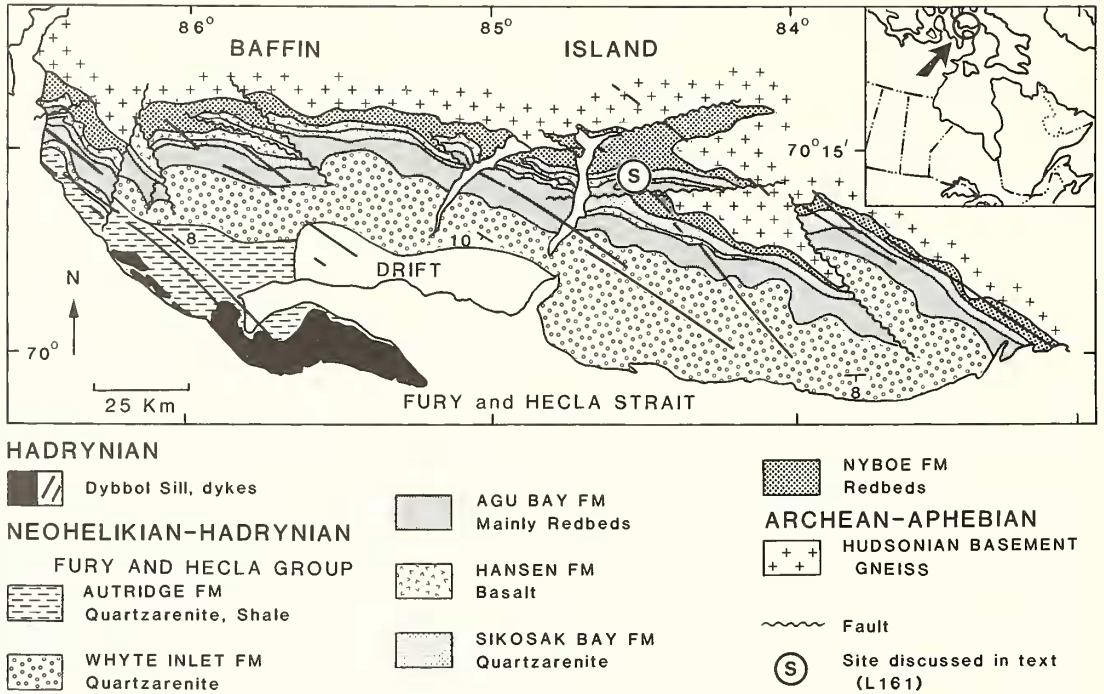
**ABSTRACT.** A shale sample from the Black Shale Member of the *c.* 1250 Ma Agu Bay Formation, Fury and Hecla Group, north-west Baffin Island contains abundant, well-preserved microfossils. The assemblage is dominated by small leiosphaerid acritarchs of which *c.* 15 per cent show structures here interpreted as medial split release structures. Colonial unicells and larger spheroidal acritarchs are uncommon, and filamentous microfossils extremely rare. A single specimen of the highly distinctive acritarch *Valeria lophostriata* extends the geographic range of this taxon and, in concert with geochronological and chemostratigraphical data, constrains the timing of Fury and Hecla deposition to the early Late Riphean. The overall habit of the Black Shale Member assemblage, including the even bedding plane distribution of fossils, supports the sedimentological and stratigraphical evidence for a mid to outer shelf depositional environment. Incorporating these findings into a review of Proterozoic shale-hosted microfossils reveals a distinct depth/diversity trend in assemblage structure such that five broad zones can be recognized extending from restricted nearshore to basinal environments. The depositional environments of the Neoproterozoic Mineral Fork Formation, Utah, and the terminal Proterozoic Pertatataka Formation, Australia, are reconsidered using this palaeoecological measure of depositional environment.

LIKE their Phanerozoic counterparts, Proterozoic microfossils are now being usefully applied in biostratigraphy (Vidal and Knoll 1983; Jankauskas 1989; Knoll and Butterfield 1989), palaeoecology, and palaeoenvironmental analysis (Ivanovskaya and Timofeev 1971; Knoll 1984; Vidal and Nystuen 1990; Knoll *et al.* 1991), as well as illuminating patterns of biotic evolution. The degree to which this is possible depends on a number of factors, including the quantity and quality of fossils and a detailed understanding of their distribution in time and space. As organic-walled microfossils in younger rocks show pronounced palaeoenvironmental partitioning (Staplin 1961; Jacobson 1979; Dorning 1981; Dale 1983) environmental effects are also to be expected in the Proterozoic. These must be eliminated from any biostratigraphical or evolutionary calculations, but a systematic documentation of such trends offers valuable insights into depositional environment, especially where other indicators are absent or ambiguous.

A shale sample from the mid to outer shelf Black Shale Member of the Proterozoic Agu Bay Formation, Fury and Hecla Group, Baffin Island, Canada contains an abundant, well-preserved microfossil assemblage. Detailed analysis of both sedimentary facies and fossil diversity and distribution permits its incorporation into a broad characterization of depth-dependent trends in Proterozoic microfossils. Individual components of the Agu Bay biota also offer useful physiological, taxonomic and, in one instance, biostratigraphical data.

## GEOLOGICAL SETTING

The Fury and Hecla Group is a *c.* 600 m thick, little altered Proterozoic sedimentary sequence overlying Hudsonian basement gneisses on northern Baffin Island (Chandler 1988) and adjacent Melville Peninsula (Schau and Beckett 1986) (Text-fig. 1). The predominantly siliciclastic succession is divided into six formations

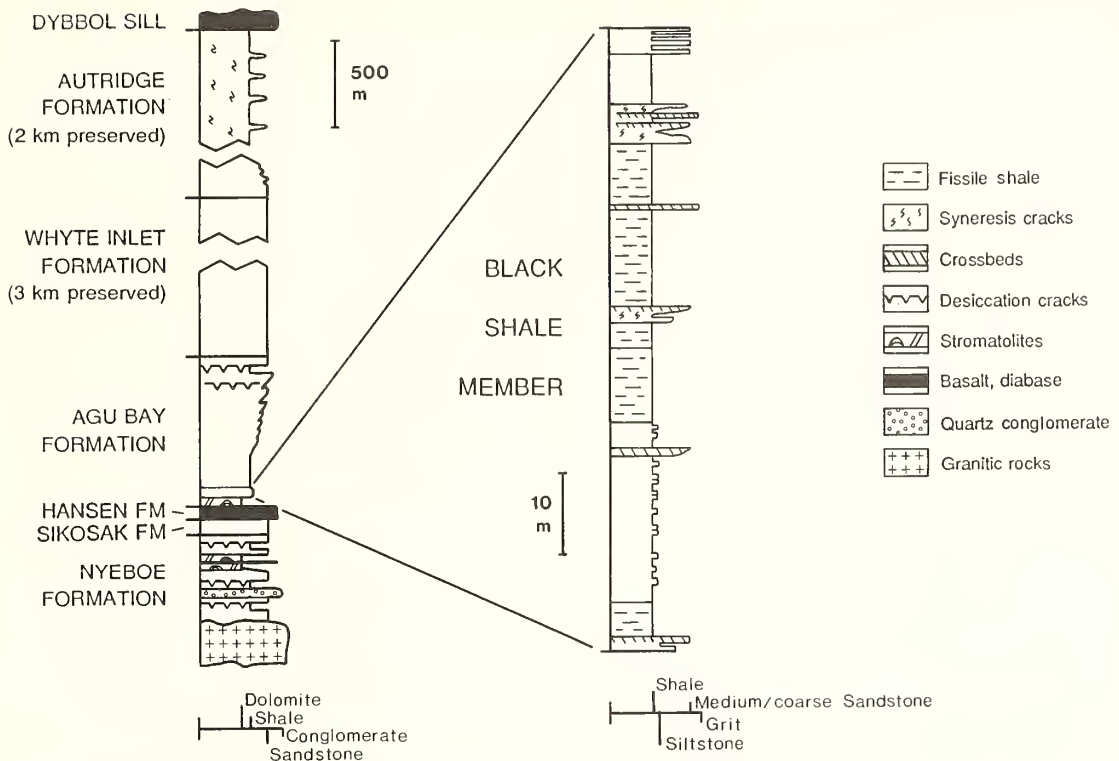


TEXT-FIG. 1. Geological map of the Fury and Hecla Group, northwestern Baffin Island, Canada, showing microfossil locality 'S'.

(Text-fig. 2) with changes in facies and unit thicknesses occurring along a strike of about 115 km: the basal Nyeboe Formation (500 m) consists largely of alluvial red quartz arenite with minor marine stromatolitic dolomite and red amygdaloidal basalt flows. It is overlain by the shallow, tidal-dominated Sikosak Formation (150+ m) and the apparently subaerial basalts of the Hansen Formation (0–30 m). However, Schau (pers. comm. 1991) considers the Hansen Formation to be a sill.

The succeeding Agu Bay Formation is c. 600 m thick and comprises three members. The basal 0–10 m thick Dolomite Member includes stromatolitic reefs, oncolites, oolites and mudcracks, indicative of shallow-subtidal to supratidal environments. The overlying and fossiliferous Black Shale Member (Text-fig. 2) represents a marked shift to deeper water deposition. It is up to 75 m thick and is dominated by friable, often rhythmically interbedded black shale and siltstone (see Chandler 1988, fig. 11*d*). Upward-coarsening and variously cross-bedded quartz arenite beds up to 2 m thick make up several per cent of the section and contain clasts that may have derived from the underlying Dolomite Member. In the absence of any shallow-water features, the overall thickness, textures and lateral continuity of the Black Shale Member point to it having been deposited largely below storm wave base on a marine shelf across which sand-bars occasionally migrated. The upper 500 m of the Agu Bay Formation, the Redbed Member, an abundantly mudcracked, shoaling coastal unit, marks a return to shallow-water conditions. Fury and Hecla Group deposition is concluded with the overlying Whyte Inlet (0–3000 m) and Autridge (2000 m) Formations, together interpreted as an upward-deepening marine shelf succession.

The Fury and Hecla Group is considered broadly correlative to several other Proterozoic sequences in the eastern arctic of North America. Good lithostratigraphical comparisons have been drawn with the Egalulik Group of the northernmost Baffin Island Bylot Supergroup, and with the Wolstenholme and Dundas Formations of the Thule Group, northwestern Greenland (Jackson and Iannelli 1981; Jackson 1986; Chandler 1988). Thick carbonate units overlie these siliciclastic rocks in both the Bylot (Uluk-san Group) and Thule (Narrsárssuk Formation) sections, but not in the Fury and Hecla Group.



TEXT-FIG. 2. Stratigraphic column of the Fury and Hecla Group and an expanded view of the Black Shale Member of the Agu Bay Formation. Fossiliferous sample L161 was collected from an incomplete section of the Black Shale Member 23 km to the east of the depicted column, thus its exact level in the Member is unknown.

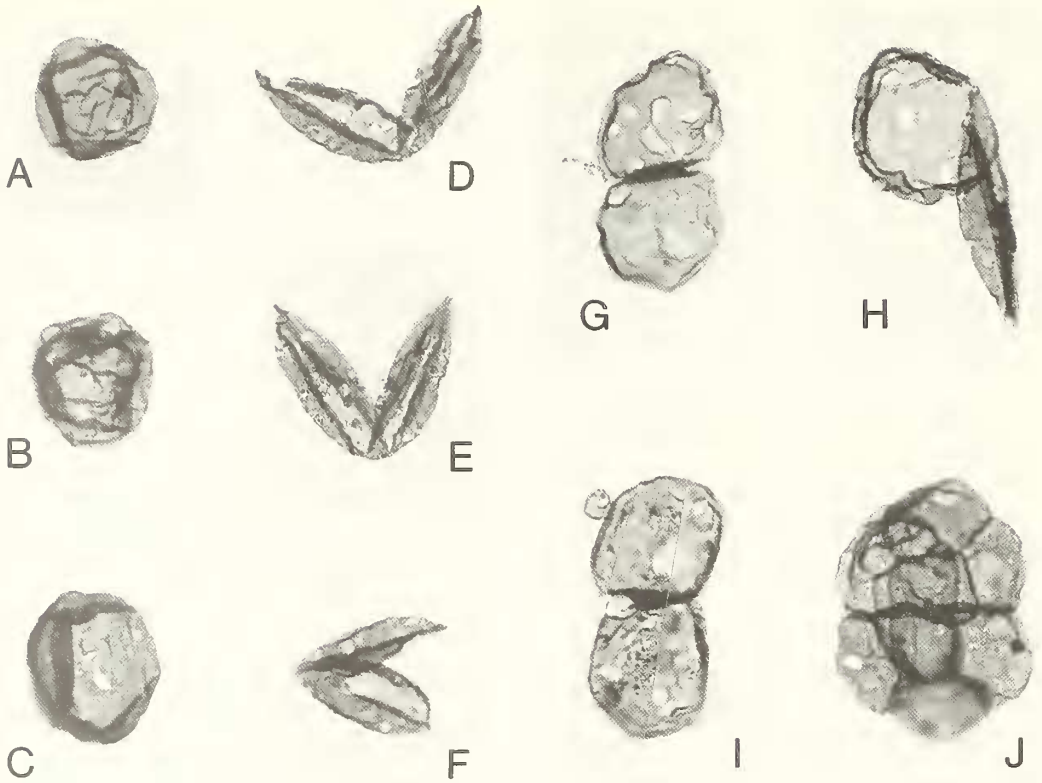
### Geochronology

The Fury and Hecla Group contains subaerial basalt flows in the Nyeboe and, probably, Hansen Formations. The two igneous units are similar lithologically and occur stratigraphically within 200 m of one another, suggesting a broadly equivalent generation. The group is topped by the Dybbol Sill and is cut by mafic dykes.

Chandler (1988, fig. 17) correlated the Hansen Formation with the Nauyat Formation basalts at the base of the Bylot Supergroup. Potassium-argon dates from the Nauyat volcanics range from  $762 \pm 26$  to  $1221 \pm 31$  Ma (Jackson and Iannelli 1981) while the Hansen basalts have yielded K-Ar ages of  $1089 \pm 32$ ,  $1117 \pm 40$  and  $1121 \pm 33$  Ma (Chandler and Stevens 1981). Fahrig *et al.* (1981) placed the palaeomagnetic pole for the Nauyat Formation at 1220 Ma. The Dybbol Sill gives K-Ar ages of  $746 \pm 87$  Ma and  $716 \pm 166$  Ma, while the dykes cutting the Fury and Hecla Group have K-Ar ages of  $643 \pm 27$  Ma and  $631 \pm 43$  Ma (Chandler and Stevens 1981).

The ages from the mafic igneous rocks in the Fury and Hecla Group coincide closely with the widespread Mackenzie and Franklin dyke swarms of the Canadian arctic (Chandler and Stevens 1981). LeCheminant and Heaman (1989) dated the Mackenzie event at  $1267 \pm 2$  Ma, and Heaman *et al.* (1992) the Franklin event at  $723 \pm 3$  Ma, both ages from U-Pb analyses on baddeleyite. Given a short duration for the Mackenzie intrusions (LeCheminant and Heaman 1989) and assuming a Mackenzie age for the red flows in the Nyeboe Formation, the above data tie Fury and Hecla Group deposition more closely to the Mackenzie than to the Franklin event, and suggest that the Agu Bay fossils are close to 1250 Ma old.

Support for a Mackenzie as opposed to a Franklin age also comes from chemostratigraphy. As the Fury and Hecla Group is dominantly siliciclastic, secular trends in carbon and strontium isotopes are not readily available. However, isotopic analysis of carbonate rocks from the broadly correlative Uluksan Group (Butterfield, Knoll and Hayes, unpublished data), and Narrsarsuk Formation (A. H. Knoll, pers. comm.



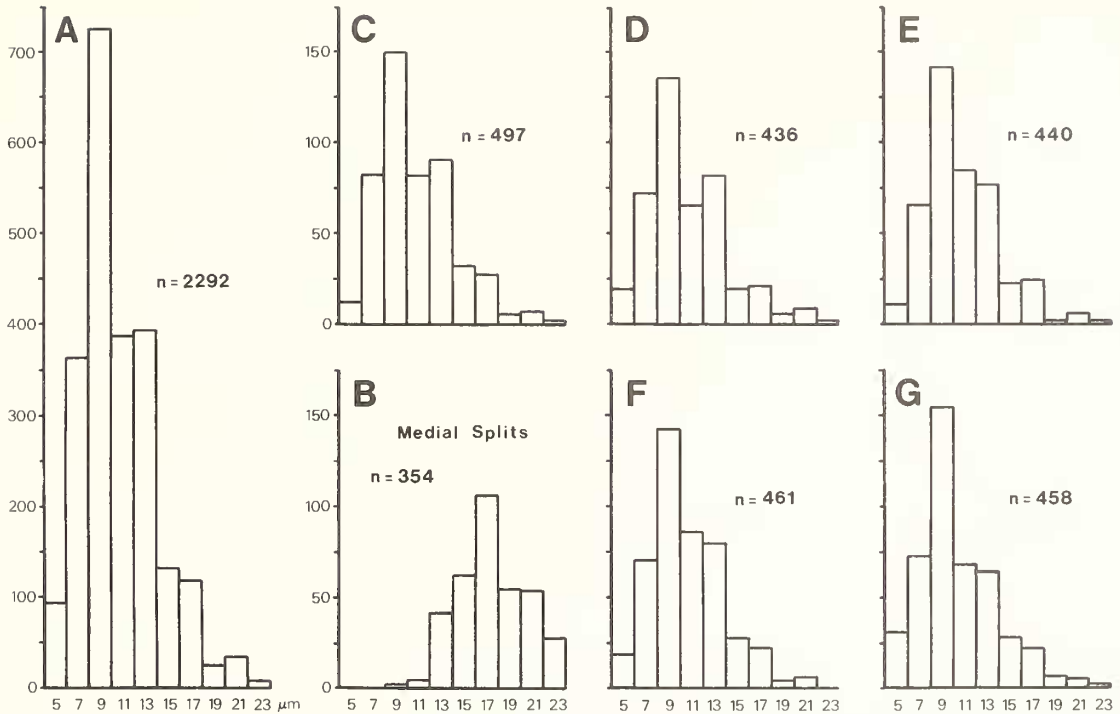
TEXT-FIG. 3. Black Shale Member microfossils. A–I, *Leiosphaeridia minutissima*, either entire (A–C) or with medial splits in various orientations (D–I); note the small leiosphaerid ( $3\ \mu\text{m}$  diameter) attached to the specimen in I. All magnifications  $\times 715$ . A, HUPC 62450; Slide L161-35. B, HUPC 62451; Slide L161-35. C, HUPC 62453; Slide L161-24. D, HUPC 62458; Slide L161-35. E, HUPC 62456; Slide L161-28. F, HUPC 62457; Slide L161-35. G, HUPC 62463; Slide L161-31. H, HUPC 62459; Slide L161-26. I, HUPC 62460; Slide L161-36. J, *Satka* (?) sp. HUPC 62468; Slide L161-25,  $\times 715$ .

1991) yield  $\delta^{13}\text{C}$  values from  $-1.0$  to  $+3.2\%$  PDB, values substantially lighter than those typical of 700–800 Ma (Franklin age) carbonates in the Canadian arctic and elsewhere (Knoll *et al.* 1986; Asmerom *et al.* 1991; Kaufman *et al.* 1992). While not definitive in themselves, these isotopic signatures are more in accord with those of older Proterozoic carbonates such as the unweathered dolomites of the 1100–1200 Ma Mescal Limestone of Arizona (Beccuas and Knauth 1985).

#### PALAEONTOLOGY

Bedding-parallel thin sections of Fury and Hecla and Group shales and siltstones were prepared for preliminary micropalaeontological examination. A single green-brown shale (sample L161) from the Black Shale Member of the Agu Bay Formation revealed abundant and very well preserved populations of spheroidal microfossils. Most of the remainder of L161 was similarly prepared, yielding sixty-seven thin-sectioned shale chips with a total area of *c.*  $40\ \text{cm}^2$ ; *c.*  $1\ \text{cm}^3$  of the sample was processed in hydrofluoric acid.

The fossil assemblage is dominated overwhelmingly by small, thin-walled and unornamented spheroidal microfossils (leiosphaerids) which provide little other than size as a distinguishing taxonomic character (Text-fig. 3A–I). A unimodal size frequency distribution ( $n = 2292$ ) skewed

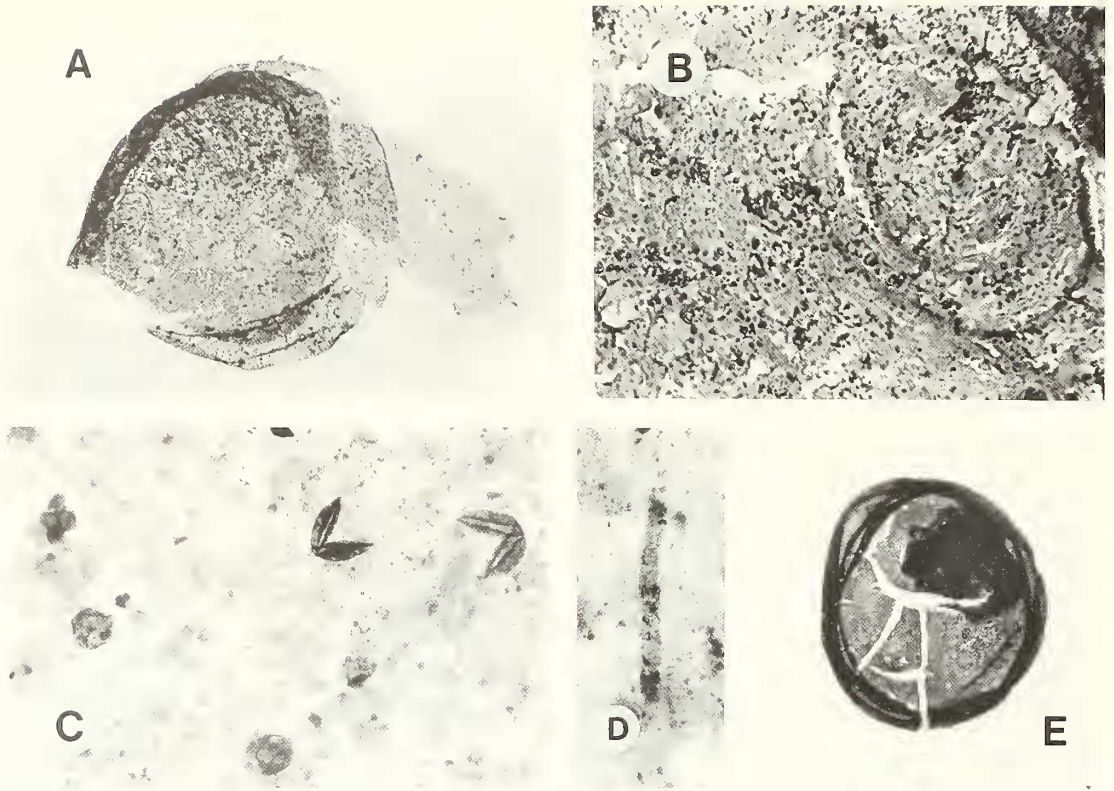


TEXT-FIG. 4. Size-frequency distribution of Black Shale Member leiosphaerids (counts from bedding-parallel thin sections). A, distribution of entire (unsplit) leiosphaerids (cumulative of histograms C–G). B, distribution of medially split leiosphaerids. C–G, distribution of five separate counts of entire leiosphaerids from five different thin sections of sample L161: C, L161-15-C; D, L161-22-C; E, L161-16-C; F, L161-7-C; G, L161-1-L.

moderately to the right (Text-fig. 4A) suggests that the population is monospecific, and a mean diameter of  $10.6 \mu\text{m}$  ( $\text{SD} = 3.65 \mu\text{m}$ ) places them within the form taxon *Leiosphaeridia minutissima* (Jankauskas 1989). Approximately 15 per cent of the population consistently exhibits medial split release structures (Text-fig. 3D–I), of which *c.* 12 per cent are orientated so that they superficially appear as cellular dyads (Text-fig. 3G, I; note the specimen in 3H in which one hemisphere was orientated 'parallel' to bedding, the other 'lateral'); the edges of the separated hemispheres are commonly enrolled. These medially-split forms fall entirely within the size range of the entire leiosphaerids, although their mean measured diameter is somewhat larger ( $\bar{x} = 17.5 \mu\text{m}$ ,  $\text{SD} = 3.03 \mu\text{m}$ ,  $n = 354$ ; Text-fig. 4B). As the planar dimensions of *split* compression fossils are typically exaggerated relative to unsplit material (Harris 1974), the closely comparable wall structure, bedding-plane distribution (see below), and size of these two forms suggest that they belong to a single population.

Other taxa in the Black Shale Member are rare, together comprising less than 1 per cent of the assemblage. These include larger spheroids measuring up to  $200 \mu\text{m}$  diameter and ascribable to the acritarch species *Leiosphaeridia crassa* and *L. jacutica* (Text-fig. 5E), and infrequent colonial spheroids that resemble *Synsphaeridium* and *Satka* (Text-fig. 3J). Only two filamentous fossils were encountered and their occurrence as short, isolated fragments in thin-section (Text-fig. 5D) identifies them as allochthons. Their preservation nevertheless suggests that the general absence of filaments in the Black Shale Member is a reflection of original distribution rather than a taphonomic bias.

The most distinctive component of the Black Shale assemblage is a single specimen of the acritarch *Valeria (Kildinosphaera) lophostriata* (Text-fig. 5A–B), characterized by its unique wall sculpture of very fine (sub-micron-spaced) concentric striae emanating from opposite 'poles'. The



TEXT-FIG. 5. Black Shale Member microfossils. A–B, *Valeria lophostriata* (HUPC 62467, Slide L161-31): A, specimen within an unornamented outer envelope,  $\times 150$ ; B, detail of A showing 'pole' and concentric striae,  $\times 925$ . C, entire and medially split leiosphaerids in bedding-parallel thin section L161-16-L (England Finder position M-19-1),  $\times 325$ . D, filament fragment in bedding-parallel thin section L161-1-L (England Finder position L-19-4),  $\times 325$ . E, *Leiosphaeridia jacutica* (HUPC 62465, Slide L161-29),  $\times 325$ .

vesicle is  $250\ \mu\text{m}$  in diameter, well within the previously reported  $60\text{--}700\ \mu\text{m}$  size range for the taxon, but it differs from all other occurrences in having a thin outer envelope ( $275\ \mu\text{m}$ ) surrounding the sculptured spheroid. This is considered an additional, rarely preserved feature and hence not a differentiating taxonomic one; its retention argues against the possibility that the specimen was reworked from older sediments.

*Valeria lophostriata* has a world-wide distribution which, in combination with its readily identifiable surface sculpture, recommends it as an important biostratigraphical marker. To date *Valeria* has been reported from the southern Urals (Jankauskas 1979), the Siberian Platform (Pjatiletov 1980; Volkova 1981), the Kola Peninsula (Liubtsov *et al.* 1988), both the Barents Sea (Vidal and Siedlecka 1983) and Tanafjord-Varangerfjord (Vidal 1981a) regions of northern Norway, the Visingsö Beds of southern Sweden (Vidal and Siedlecka 1983), the Chuar and Uinta Mountain Groups of the southwestern USA (Vidal and Ford 1985), the Thule Group of northwestern Greenland (Dawes and Vidal 1985), and southern Africa (A. H. Knoll, pers. comm. 1991). In all instances it is temporally restricted to the Late Riphean, and it occurs most characteristically during the first one-third of that period (Liubtsov *et al.* 1988, table 15; Jankauskas 1989, table 4). The discovery of *Valeria* in the Agu Bay Formation corroborates the geochronological evidence for an early Late Riphean deposition of Fury and Hecla sediments. Moreover, its similar occurrence in the Wolstenholme and Dundas Formations on northwest

Greenland (Dawes and Vidal 1985) substantially reinforces the lithostratigraphical and chemostratigraphical data correlating the Thule Group with the Fury and Hecla Group (see above).

### *Palaeobiology*

As organisms, the larger spheroidal microfossils of the Agu Bay Black Shale assemblage can be reasonably identified as some life cycle stage of protistan grade, probably photosynthetic eukaryotes. In contrast, the small simple leiosphaerids that comprise the majority of the Agu Bay fossils are not immediately identifiable at even the kingdom or superkingdom level. The occurrence of medial splits in spheroids has conventionally been taken as evidence of eukaryotic grade (e.g. Green *et al.* 1989), but such structures are also found in baeocyte-releasing pleurocapsalean cyanobacteria (Waterbury and Stanier 1978, fig. 4) and the germinating akinetes of various filamentous cyanobacteria (Nichols and Adams 1982). The overall habit of these cyanophytes is nevertheless distinct from the Agu Bay fossils: pleurocapsaleans live as attached benthic organisms, often with distinctive patterns of cell division, while akinetes are generally associated with filamentous growth. The medially split, filament-free, and fully planktic (see below) habit of the Agu Bay *L. minutissima* fossils supports their interpretation as eukaryotes.

Finer biological analysis of these small spheroidal fossils is frustrated by their morphological simplicity. Nonetheless, additional palaeobiological information can often be gleaned from the details of fossil distribution and orientation, i.e. preserved 'behaviour' (e.g. Butterfield *et al.* 1988; Green *et al.*, 1988, 1989). Unfortunately, the conventional procedure for studying shale-hosted microfossils, palynological maceration, necessarily destroys such potentially instructive information. The *in situ* (i.e. thin-section) analysis of the Agu Bay fossils allowed a detailed assessment of their original bedding-plane distribution (Text-fig. 5C). Five separate counts of c. 500 leiosphaerids (from five separate thin-sections of sample L161 recording all fossils encountered during a systematic scan) were remarkably consistent (Text-fig. 4C–G), and a Kolmogorov–Smirnov analysis of the size–frequency distributions indicated that all five samples were drawn from the same population. The abundance of fossils varies somewhat between different laminae but averages c.  $63 \text{ mm}^{-2}$  (SD =  $15 \text{ mm}^{-2}$ ) (= c.  $1000 \text{ mm}^{-3}$ ). Within any single lamina fossil distribution is much more uniform. For example, fossils on five randomly chosen  $1 \text{ mm}^2$  plots of thin-section L161–16C showed an Index of Dispersion ( $s^2/\bar{x}$ :  $6.2/78.8 = 0.078$ ) significantly less than unity (> 99% confidence), indicating their very even distribution on individual bedding planes (cf. Odum 1971; Rosenberg 1974), a distribution that could only have derived from dispersed plankton settling out of a water column (Vidal and Knoll 1983). The organisms preserved in the Black Shale Member were not only eukaryotic but planktic.

These small leiosphaerids are comparable to the degradation-resistant resting/dispersal stages of various algae which often show similar medial-split excystment structures (e.g. Dale 1983; Margulis *et al.* 1988). Alternatively, they might be interpreted simply as the cell walls and cast-off cell walls of an actively growing unicellular alga. Cells of the extant green alga *Chlorella*, for example, fall within the morphological range of the fossil population, and some species develop highly resistant sporopollenin-bearing walls (Atkinson *et al.* 1972; Rascio *et al.* 1979). The *Chlorella* life cycle also involves the production of intracellular autospores which, upon reaching maturity, are released from the mother cell via a medial split (Atkinson *et al.* 1972, fig. 21). Interestingly, the split edges of a vacated *Chlorella* mother cell tend to curl in on themselves very much in the manner of the medially split fossils (Text-fig. 3D–F); a small spheroid attached to a larger, medially split leiosphaerid (Text-fig. 3I) is interpreted as a possible daughter autospore. These Agu Bay leiosphaerids may thus as likely represent a population of physiologically active unicellular algae as one of dormant cysts or spores.

### PALAEOENVIRONMENTAL DISTRIBUTION

Fossil biotas play an important role in determination of palaeoenvironments of Phanerozoic sediments (Boucot and Carney 1981), but similar application in Proterozoic sequences has not been

generally exploited. For carbonate facies with their diverse and relatively diagnostic sedimentary structures this may not present much of an impediment, and stromatolitic facies offer palaeoenvironmental indicators down to the base of the photic zone (Hoffman 1976). In contrast, fine-grained siliciclastic sediments occur from terrestrial to abyssal environments and, in the absence of biological markers, can often not be constrained to particular palaeoenvironmental settings. Microfossils are commonly preserved in Proterozoic shales and a detailed understanding of their spatial distribution offers a potentially valuable measure of palaeoenvironment.

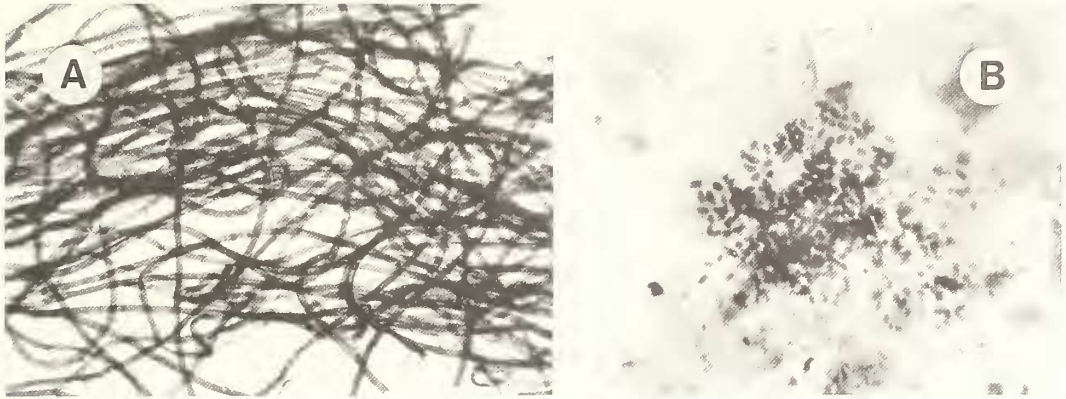
Just as all shales are not necessarily distal and deep water, all shale-hosted Proterozoic microfossils did not occupy a common ecological niche. Indeed, most such assemblages are reported from relatively shallow water facies (Vidal 1981*b*; Vidal and Knoll 1983). For example, shallow subtidal shales from the 750–850 Ma Wynniatt Formation on Victoria Island, arctic Canada (Butterfield and Rainbird 1988), and the marginally younger Svanbergfjellet Formation of Spitsbergen (Butterfield *et al.* 1988) preserve abundant and diverse microfossils. Unlike the Agu Bay Black Shale material, bedding-parallel thin sections of these rocks reveal localized populations and associations of microfossils and abundant, often mat-forming filaments (Text-fig. 6). This patchy and otherwise autochthonous distribution indicates an important contribution by benthic (Rosenberg 1974), probably photosynthetic, organisms.

Shallow-water shale biotas of Proterozoic age tend to be taxonomically diverse and typically include a variety of large (50–3000  $\mu\text{m}$  diameter) spheroidal acritarchs, set amongst an almost ubiquitous background of small leiosphaerids. Strongly ornamented Proterozoic acritarchs were dominantly, if not exclusively, shallow-water inhabitants (Knoll and Butterfield 1989; Vidal 1990; Jenkins *et al.* 1992). However, perhaps the most regularly recurring constituents of these shallow-water assemblages are filamentous microfossils comparable to modern LPP-type cyanobacteria. These are best known as the unambiguously autochthonous and photosynthetic builders of stromatolites, but they also commonly occur in fine-grained siliciclastic environments where they likewise constructed extensive microbial mats (Text-fig. 6A) (Hermann 1974; Peat *et al.* 1978; Schieber 1986; Butterfield *et al.* 1988). That they were benthic and photosynthetic is supported by their usual occurrence in demonstrably shallow-water sediments, and a negative correlation between filament abundance and depth (Horodyski 1980; Knoll and Swett 1985). It is of course conceivable that some filaments were planktic; however, the general absence of LPP-type filaments in offshore environments, both in the modern oceans (Fogg 1982) and in Phanerozoic acritarch-preserving sediments, argues against such an interpretation. Alternatively, fossil filaments may simply be transported and redeposited shallow-water benthos, as appears likely for the very rare filament fragments in the Agu Bay shale. Nonetheless, their consistent appearance in shallow-water sediments and conspicuous absence from deeper water environments reflects at least a broad palaeoenvironmental partitioning.

In contrast, distal shelf to slope microbiotas in the Proterozoic are characterized by taxonomically depauperate assemblages of small but often very abundant spheroidal microfossils, generally assignable to *Sphaerocongregus* (= *Bavlinella*); both filaments and larger acritarchs are typically absent (e.g. Moorman 1974; Mansuy and Vidal 1983; Vidal and Siedlecka 1983; Palacios 1989; Vidal and Nystuen 1990). Vidal and Nystuen (1990) further suggested that acritarch-producing eukaryotic plankton probably did not occupy these distal, open ocean environments during the Proterozoic.

The facies analysis of the Agu Bay Black Shale Member (Chandler 1988) places it intermediate between the mid and the outer shelf; the Black Shale Member fossils also show an intermediate character. Deep water influence is indicated by the low diversity, high abundance and entirely allochthonous nature of the assemblage, and that of shallower water by the dominance of eukaryotic organisms and the presence of at least a few larger acritarchs and rare filament fragments. Thus, the Black Shale Member fossil assemblage provides an independent measure of the mid to outer shelf palaeoenvironment. More importantly, it appears that the overall character of a Proterozoic shale palaeontological assemblage, particularly as it may be corroborated by a





TEXT-FIG. 6. Characteristic aspect of microfossil assemblages in shallow-water (i.e. photic zone) Proterozoic shales: A, abundant LPP-like filaments; B, patchy distribution indicative of benthic growth. Both examples from peristromatolitic shales of the c. 750 Ma Wynnatt Formation, Victoria Island, Canada,  $\times 360$ .

number of distributional and dominance criteria, can be used in assessing depositional environments, in the absence of reliable sedimentological evidence.

The palaeontological, and hence palaeoenvironmental, onshore-offshore gradient in late Proterozoic proximal carbonate sequences has been discussed in detail by Knoll (1984) and Knoll *et al.* (1991). Here, the highest diversity was met in the most 'distal' open-water conditions in apparent reversal of the trend observed in siliciclastic environments. This derives simply from the differences of scale. Most shallow-water shales can be considered indicative of relatively unrestricted, usually subtidal settings and will therefore correspond broadly with the open-water, but nevertheless shallow-water facies of the carbonate studies; indeed, the two shallow open-water environments share a significant number of both benthic microbial and acritarch taxa (see references in Knoll 1984; Butterfield *et al.* 1988). Similarly, restricted intertidal to supratidal shales are likely to preserve low-diversity assemblages of autochthonous (patchily distributed) prokaryotes, comparable to the microbial mat biotas of restricted carbonate environments. Thus, shale-hosted fossil assemblages can be applied to palaeoenvironmental analysis in the same manner as those in carbonate facies. In addition, since fossiliferous shales are not limited to shallow-water, peristromatolitic facies, they offer an excellent opportunity to extend the palaeontological characterization of Proterozoic basins out across the shelf and slope. Systematic trends in Proterozoic microfossil occurrence and distribution can be usefully categorized into five broad environmental zones (Text-fig. 7):

1. *Near shore restricted, lagoonal to supratidal*: fossils dominantly autochthonous (i.e. patchy bedding plane distribution); abundant filaments and/or small spheroids; dominantly prokaryotic; low diversity. The microfossils of this facies are best known from silicified microbial mat material of carbonate environments although they might well occur in intertidal or lagoonal shales.

2. *Near shore unrestricted, shallow subtidal*: fossils both autochthonous and allochthonous (planktic); abundant filaments; moderate to high diversity of large ( $> 50 \mu\text{m}$  diameter) acritarchs; if of appropriate age, large process-bearing acritarchs. Examples: McMinn Formation (Peat *et al.* 1978); Wynnatt Formation (Butterfield and Rainbird 1988); Svanbergfjellet Formation (Butterfield *et al.* 1988); Rodda Beds-Murnaroo-1 drillhole (Jenkins *et al.* 1992). Comparable distribution of large complex acritarchs is found in open-water carbonate environments where they likewise occur with benthic microbial mats (e.g. Knoll 1984; Awramik *et al.* 1985; Allison and Awramik 1989; Yin 1990; Knoll 1992).

3. *Mid shelf, moderate depth (lower photic zone)*: fossils dominantly allochthonous (i.e. even distribution on bedding planes); moderate diversity of spheroidal acritarchs but no substantially

ornamented forms; sparse filaments. Examples: Chamberlain Shale (Horodyski 1980); Glasgow-green Formation (Knoll and Swett 1985); Arcoona Quartzite Member of the Tent Hill Formation (Damassa and Knoll 1986. This is a lateral equivalent of the Pertatataka Formation discussed below).

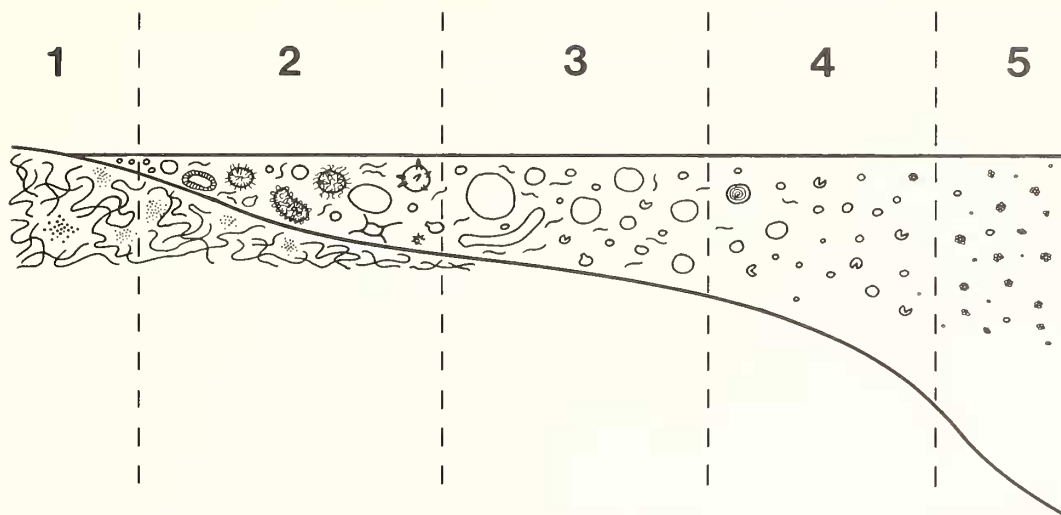
4. *Mid to outer shelf, deep water (sub photic zone)*: fossils entirely allochthonous; low taxonomic diversity, dominated by moderate to small ( $< 50 \mu\text{m}$ ) diameter spheroids; eukaryotes common; filaments rare (wash-ins?) to absent. Examples: Biri Formation (Vidal and Nystuen 1990); Black Shale Member of the Agu Bay Formation (present study).

5. *Slope to basinal, turbidite dominated environments, deep water*: fossils entirely allochthonous; often very abundant; very low taxonomic diversity; unambiguous eukaryotes absent; filaments absent. Assemblages are typically monospecific, composed exclusively of planktic prokaryotes with growth series similar to *Sphaerocongregus* Moorman. Examples: Hector Formation (Moorman 1974); the Brioverian of France (Mansuy and Vidal 1983); Bøttrum Formation (Vidal and Nystuen 1990).

Microfossil distribution as a means of deciphering palaeoenvironment is subject to a number of caveats: (1) superior fossil preservation is necessary for any meaningful analysis; (2) local circumstances may impinge upon the generalized pattern, particularly in nearshore settings where sediment input and salinity are likely to be variable; (3) secular changes in fossil distribution must be accommodated and (4) as benthic organisms are not exclusively photosynthetic, bedding-plane distribution alone offers only a one-tailed test for allochthony. Clearly no one feature is sufficient for determining palaeoecology (and thereby palaeoenvironment); rather, it derives from an overall analysis of a fossil assemblage, incorporating all available palaeontological and, of course, sedimentological data. Because the scheme presented here is based on the extremely conservative prokaryotic components of a biota and broad grades of eukaryotic organization (thus eliminating evolutionary effects), it should be applicable to most of the middle and late Proterozoic. It is limited on the one hand by the evolution of eukaryotic plankton, and on the other by the decline of organic-walled fossil preservation associated with the appearance of bioturbating animals. Despite its obvious simplification, the distribution shown in Text-figure 7 accords with a majority of Proterozoic microfossil assemblages.

If the above characterization is generally applicable, it should help to resolve the palaeoenvironmental setting of Proterozoic sequences in which the sedimentological context is ambiguous or in dispute. For example, the Neoproterozoic Mineral Fork Formation in Utah has been interpreted both as a terrestrial to shallow marine glaciogene unit (Crittenden *et al.* 1952; Knoll *et al.* 1981), and as a distal shelf sequence involving submarine mud and debris flows (Condie 1967; Schermerhorn 1974). Relatively deep-water glacio-marine conditions are now thought to have prevailed during most of Mineral Fork deposition but a detailed account of the constituent facies is not yet available (Christie-Blick 1983). Knoll *et al.* (1981) reported a microfossil assemblage from fine-grained facies of the Mineral Fork Formation that from a thin-section study appear to be entirely planktic, includes no fossil filaments, and is dominated by abundant small spheroids. To a remarkable degree the biota replicates the form and distribution of *Sphaerocongregus* in the distal, deep-water Hector Formation (Moorman 1974). Moreover, it differs conspicuously from other Neoproterozoic tillite-associated microbiotas which typically include a number of larger acritarch taxa (e.g. Vidal 1976, 1979, 1981*a*). Thus, the palaeontological data would argue that at least the fine-grained Mineral Fork facies were deposited in water sufficiently deep to preclude benthic photosynthesizers, and sufficiently distal to preclude influx of filaments and acritarch-forming eukaryotes (our zone 5).

At the other end of the scale, the very late (post-Varangian) Proterozoic Pertatataka Formation of central Australia has been described as a deep-water distal turbidite (Korsch 1986; Zang 1988; Zang and Walter 1989) yet, palaeontologically, it contains one of the most diverse assemblages of large, morphologically complex acritarchs so far described. If this environmental interpretation is



TEXT-FIG. 7. Diagram illustrating the palaeoenvironmental distribution of Proterozoic microfossils from restricted near-shore (zone 1) through distal shelf and slope (zone 5) environments. Figures below the base-line represent non-randomly distributed and/or filamentous benthos limited to the photic zone. The large ornamented plankton in zone 2 are limited to the pre-Ediacaran late Proterozoic. The Black Shale Member of the Agu Bay Formation represents a zone 4 assemblage.

correct, it clearly contradicts the palaeoecological pattern outlined above. It is worth noting, however, that the high acritarch diversity in the Pertatataka Formation occurs consistently at the top of the sequence where it appears to be overlain conformably by the oolitic and stromatolitic (photic zone) carbonates of the Julie Formation (Wells *et al.* 1970; Preiss *et al.* 1978; Lindsay and Korsch 1991). The diverse acritarchs furthermore occur with a variety of well-preserved filaments (Zang 1988; Zang and Walter 1989) which in some cases are recovered as entangled, laterally continuous mats (Zang 1988, pl. 103, figs b–d). Conversely, filaments are conspicuously absent in the middle and lower parts of the Pertatataka Formation, and the acritarch assemblage becomes systematically less diverse down section (Zang 1988). At least in some areas, the lower Pertatataka Formation is dominated by small spheroids with growth sequences comparable to *Sphaerocongregus* (Zang and Walter 1989), very similar to turbidite-hosted biotas elsewhere. Thus, the distribution of microfossils argues strongly for a more distal, deeper-water environment at the base of the Pertatataka Formation (our zone 5 or 4), but shallowing upwards to well within the photic zone in the upper parts where the diverse acritarchs and filamentous microfossils occur (our zone 2) (see Lindsay and Korsch 1991). Comparable ornamented acritarchs in correlative units of the Officer Basin, South Australia are limited to nearshore facies (Jenkins *et al.* 1992).

Palaeoenvironmental information is also essential for making accurate biostratigraphic correlations. There is good potential for a rigorous, acritarch-based biostratigraphy of at least the late Proterozoic (Knoll and Butterfield 1989). It is also clear that the morphologically complex forms upon which such a scheme must necessarily be based have relatively restricted palaeoenvironmental distributions – most occur in shallow-water (our zone 2) environments. Before meaningful biostratigraphical correlations can be made, it must be evident that similar palaeoecosystems are being compared. For example, the c. 1300 Ma McMinn Formation of central Australia was clearly deposited under shallow marine conditions as is indicated by both its sediments (Peat *et al.* 1978) and the character of its preserved fossils, i.e. abundant filaments, entangled filamentous mats and large acritarchs. Thus, the absence of morphologically complex acritarchs typical of 900–600 Ma shallow-water sequences indicates an evolutionary rather than an environmental control on taxonomic composition and is consequently of biostratigraphical

significance. In contrast, the trend from low to intermediate to high diversities (and simple to complex morphologies) of acritarchs observed going up section through the Pertatataka Formation (Zang 1988, text-fig. 4–16; Zang and Walter 1989) appears to be one of simple palaeoenvironmental change, i.e. a shallowing upward sequence.

### CONCLUSION

Proterozoic fossils clearly have distributions that vary systematically in both space and time. Their full potential as palaeoenvironmental and biostratigraphical tools nevertheless rests on our ability to distinguish the two accurately. Thus, forms that have previously been applied biostratigraphically, such as *Sphaerocongregus*, appear to be more palaeoenvironmentally than temporally controlled, while large process-bearing acritarchs offer useful constraints in both dimensions. Leiosphaerid acritarchs, the signature plankton of the Proterozoic, may also reveal important stratigraphical and environmental information under appropriate analysis. Thus, prokaryote-dominated zones 1 and 5 may be distinguished on the basis of bedding-plane distribution (patchy as opposed to even) and the prevalence of filamentous microfossils. In the same way, zone 2 leiosphaerid assemblages of middle Proterozoic age (prior to the evolution of ornamented acritarchs) may be distinguished from superficially similar late Proterozoic zone 3 assemblages through indications of benthic growth.

Palaeoenvironmental and biostratigraphical analysis involve different approaches to the fossil record. The latter demands morphologically distinctive forms but a single specimen can often provide significant temporal resolution, such as the Agu Bay *Valeria*. Conversely, palaeoecology, as a proxy for palaeoenvironment, is determined from large populations and overall 'community' structure. The depth-dependent characterization of Proterozoic microfossil assemblages outlined in this paper is in this sense 'community'-based, using aspects such as diversity, abundance/dominance, and spatial distribution, as well as direct, moderately reliable indicators of depth such as filamentous mats. As with their Phanerozoic counterparts, it is becoming increasingly clear that detailed investigation of Proterozoic microfossils can provide significant constraints on age, palaeoenvironment, and evolutionary history.

*Acknowledgements.* We thank the Polar Continental Shelf Project (Canada) for helicopter and communications support on Baffin Island. R. Buick and A. H. Knoll reviewed the manuscript and made a number of helpful suggestions, as did an anonymous reviewer. N.J.B. was financially supported by an NSERC postgraduate scholarship and DOE Grant DE-FG02-88ER13978 (to A. H. Knoll). This paper is Geological Survey of Canada Contribution 222091.

### REFERENCES

- ALLISON, C. W. and AWRAMIK, S. M. 1989. Organic-walled microfossils from earliest Cambrian or latest Proterozoic Tindir Group rocks, northwest Canada. *Precambrian Research*, **43**, 253–294.
- ASMEROM, Y., JACOBSEN, S. B., KNOLL, A. H., BUTTERFIELD, N. J. and SWETT, K. 1991. Strontium isotopic variations of Neoproterozoic seawater: implications for crustal evolution. *Geochimica et Cosmochimica Acta*, **55**, 2883–2894.
- ATKINSON, A. W. JR., GUNNING, B. E. S. and JOHN, P. C. L. 1972. Sporopollenin in the cell wall of *Chlorella* and other algae: ultrastructure, chemistry, and incorporation of <sup>14</sup>C-acetate, studied in synchronous cultures. *Planta*, **107**, 1–32.
- AWRAMIK, S. M., MCMENAMIN, D. S., YIN, C., ZHAO, Z., DING, Q. and ZHANG, S. 1985. Prokaryotic and eukaryotic microfossils from a Proterozoic/Phanerozoic transition in China. *Nature*, **315**, 655–658.
- BEEUNAS, M. A. and KNAUTH, L. P. 1985. Preserved stable isotopic signature of subaerial diagenesis in the 1·2-b.y. Mescal Limestone, central Arizona: implications for the timing and development of a terrestrial plant cover. *Geological Society of America, Bulletin*, **96**, 737–745.
- BOUCOT, A. J. and CARNEY, R. S. 1981. *Principles of benthic marine paleontology*. Academic Press, New York, 463 pp.

- BUTTERFIELD, N. J. and RAINBIRD, R. H. 1988. The paleobiology of two Proterozoic shales. *Geological Society of America, Abstracts with Programs*, **20**, A103.
- KNOLL, A. H. and SWETT, K. 1988. Exceptional preservation of fossils in an Upper Proterozoic shale. *Nature*, **334**, 424–427.
- CHANDLER, F. W. 1988. Geology of the late Precambrian Fury and Hecla Group, northwest Baffin Island, District of Franklin. *Geological Survey of Canada, Bulletin*, **370**, 1–30.
- and STEVENS, R. D. 1981. Potassium–argon age of the Late Proterozoic Fury and Hecla Formation, Northwest Baffin Island, District of Franklin. *Geological Survey of Canada, Paper*, **81-1A**, 37–40.
- CHRISTIE-BLICK, N. 1983. Glacial-marine and subglacial sedimentation, Upper Proterozoic Mineral Fork Formation, Utah. 703–775. In MOLNIA, B. F. (ed.). *Glacial-marine sedimentation*. Plenum Press, New York, 844 pp.
- CONDIE, K. C. 1967. Petrology of the Late Precambrian tillite (?) association in northern Utah. *Geological Society of America, Bulletin*, **78**, 1317–1344.
- CRITTENDEN, M. D. JR., SHARP, B. J. and CALKINS, F. C. 1952. Geology of the Wasatch Mountains east of Salt Lake City, Parley Canyon to Traverse Range. *Utah Geological and Mineralogical Survey Guidebook to the Geology of Utah*, **8**, 1–37.
- DALE, B. 1983. Dinoflagellate resting cysts: 'benthic plankton'. 69–136. In FRYXELL, G. R. (ed.). *Survival strategies of the algae*. Cambridge University Press, Cambridge, 154 pp.
- DAMASSA, S. P. and KNOLL, A. H. 1986. Micropalaeontology of the Late Proterozoic Arcoona Quartzite Member of the Tent Hill Formation, Stuart Shelf, South Australia. *Alcheringa*, **10**, 417–430.
- DAWES, P. R. and VIDAL, G. 1985. Proterozoic age of the Thule Group: new evidence from microfossils. *Gronlands Geologiske Undersogelse, Rapport*, **125**, 22–28.
- DORNING, K. J. 1981. Silurian acritarch distribution in the Ludlovian shelf sea of South Wales and the Welsh Borderland. 31–36. In NEALE, J. W. and BRASIER, M. D. (eds). *Microfossils from Recent and fossil shelf seas*. Ellis Horwood, Chichester, 380 pp.
- FAHRIG, W. F., CHRISTIE, K. W. and JONES, D. L. 1981. Paleomagnetism of the Bylot Basins: evidence for MacKenzie Continental tensional tectonics. In CAMPBELL, F. H. A. (ed.). *Proterozoic basins of Canada*. *Geological Survey of Canada, Paper*, **81-11**, 301–312.
- FOGG, G. E. 1982. Marine plankton. 491–513. In CARR, N. G. and WHITTON, B. A. (eds). *The biology of cyanobacteria*. University of California Press, Berkeley, 680 pp.
- GREEN, J. W., KNOLL, A. H. and SWETT, K. 1988. Microfossils from oolites and pisolites of the Upper Proterozoic Eleonore Bay Group, central East Greenland. *Journal of Paleontology*, **62**, 835–852.
- — — — — 1989. Microfossils from silicified stromatolitic carbonates of the Upper Proterozoic Limestone–Dolomite 'Series', central East Greenland. *Geological Magazine*, **126**, 567–585.
- HARRIS, T. M. 1974. *Williamsoniella lignieri*: its pollen and the compression of spherical pollen grains. *Palaeontology*, **17**, 125–148.
- HEAMAN, L. M., LECHEMINANT, A. N. and RAINBIRD, R. H. 1992. Nature and timing of Franklin igneous events, Canada: implications for a late Proterozoic mantle plume and the break-up of Laurentia. *Earth and Planetary Science Letters*, **109**, 117–131.
- HERMANN, T. N. 1974. Nakhodki massovykh skopenii trikhomov v Rifee. 6–10. In TIMOFEEV, B. V. (ed.). *Mikrofitofossilii Proterozoiia i Rannego Paleozoiia SSSR*. Nauka, Leningrad, 80 pp. [In Russian].
- HOFFMAN, P. 1976. Environmental diversity of middle Precambrian stromatolites. 599–611. In WALTER, M. R. (ed.). *Stromatolites*. Elsevier, Amsterdam, 790 pp.
- HORODYSKI, R. J. 1980. Middle Proterozoic shale-facies microbiota from the lower Belt Supergroup, Little Belt Mountains, Montana. *Journal of Paleontology*, **54**, 649–663.
- IVANOVSKAYA, A. V. and TIMOFEEV, B. V. 1971. Relationship between salinity and distribution of phytoplankton. *Geologiya i Geofizika*, **8**, 113–117. [In Russian].
- JACKSON, G. D. 1986. Notes on the Proterozoic Thule Group, northern Baffin Bay. *Geological Survey of Canada, Paper*, **86-1A**, 541–552.
- and IANNELLI, T. R. 1981. Rift-related cyclic sedimentation in the Neohelikian Borden Basin, Northern Baffin Island. In CAMPBELL, F. H. A. (ed.). *Proterozoic basins of Canada*. *Geological Survey of Canada, Paper*, **81-10**, 269–302.
- JACOBSON, S. R. 1979. Acritarchs as paleoenvironmental indicators in Middle and Upper Ordovician rocks from Kentucky, Ohio, and New York. *Journal of Paleontology*, **53**, 1197–1212.
- JANKAUSKAS, T. V. 1979. Srednerifeiskaia mikrobiota Iuzhnovo Urala i Bashkirskovo Priuralia. *Doklady Akademii Nauk SSSR*, **248** (1), 190–193. [In Russian].
- (ed.). 1989. *Mikrofitofossilii Dokembriia SSSR*. Nauka, Leningrad, 188 pp. [In Russian].

- JENKINS, R. J. F., MCKIRDY, D. M., FOSTER, C. B., O'LEARY, T. and PELL, S. D. 1992. The record and stratigraphic implications of organic-walled microfossils from the Ediacaran (terminal Proterozoic) of South Australia. *Geological Magazine*, **129**, 401–410.
- KAUFMAN, A. J., KNOLL, A. H. and AWRAMIK, S. M. 1992. Biostratigraphic and chemostratigraphic correlation of Neoproterozoic sedimentary successions: Upper Tindir Group, northwestern Canada, as a test case. *Geology*, **20**, 181–185.
- KNOLL, A. H. 1984. Microbiotas of the late Precambrian Hunnberg Formation, Nordaustlandet, Svalbard. *Journal of Paleontology*, **58**, 131–162.
- 1992. Vendian microfossils in metasedimentary cherts of the Scotia Group, Prins Karls Forland, Svalbard. *Palaeontology*, **35**, 751–774.
- , BLICK, N. and AWRAMIK, S. M. 1981. Stratigraphic and ecologic implications of late Precambrian microfossils from Utah. *American Journal of Science*, **281**, 247–263.
- and BUTTERFIELD, N. J. 1989. New window on Proterozoic life. *Nature*, **337**, 602–603.
- , HAYES, J. M., KAUFMAN, A. J., SWETT, K. and LAMBERT, I. B. 1986. Secular variation in carbon isotope ratios from Upper Proterozoic successions of Svalbard and East Greenland. *Nature*, **321**, 1–7.
- and SWETT, K. 1985. Micropalaeontology of the late Proterozoic Veteranen Group, Spitsbergen. *Palaeontology*, **28**, 451–473.
- and MARK, J. 1991. Palaeobiology of a Neoproterozoic tidal flat/lagoonal complex: the Draken Conglomerate Formation, Spitsbergen. *Journal of Paleontology*, **65**, 531–570.
- KORSCH, R. 1986. Pertatataka Formation. 103–107. in KENNARD, J. M., NICOLL, R. S. and OWEN, M. (eds). *Field Excursion 25B, 12th International Sedimentological Congress*. Bureau of Mineral Resources, Geology and Geophysics, Canberra.
- LECHEMINANT, A. N. and HEAMAN, L. M. 1989. Mackenzie igneous events, Canada: Middle Proterozoic hotspot magmatism associated with ocean opening. *Earth and Planetary Science Letters*, **96**, 38–48.
- LINDSAY, J. F. and KORSCH, R. J. 1991. The evolution of the Amadeus Basin, central Australia. *Bureau of Mineral Resources, Geology and Geophysics, Bulletin*, **236**, 7–32.
- LIUBTSOV, V. V., MIKHAILOVA, N. S. and PREDOVSKII, A. A. 1989. Vyvody. 80–82. In MITROFANOV, F. P. and JANKAUSKAS, T. V. (eds). *Litostratigrafiia i mikrofosilii pozdnego Dokenbria Kolskogo Poluostrova*. Kolskii Nauchnyi Tsent, Apatity, 129 pp. [In Russian].
- MANSUY, C. and VIDAL, G. 1983. Late Proterozoic Brioverian microfossils from France: taxonomic affinity and implications of plankton productivity. *Nature*, **302**, 606–607.
- MARGULIS, L., HINKLE, G., MCKHANN, H., MOYNIHAN, B. and BROWN, S. W. 1988. *Mychonastes desiccatus* Brown sp. nova (Chlorococcales, Chlorophyta) – an intertidal alga forming achlorophyllous desiccation-resistant cysts. *Archiv für Hydrobiologie, Supplement*, **78**, 425–446.
- MOORMAN, M. 1974. Microbiota of the late Proterozoic Hector Formation, southwestern Alberta, Canada. *Journal of Paleontology*, **48**, 524–539.
- NICHOLS, J. M. and ADAMS, D. G. 1982. Akinetes. 387–412. In CARR, N. G. and WHITTON, B. A. (eds). *The biology of cyanobacteria*. University of California Press, Berkeley, 688 pp.
- ODUM, E. P. 1971. *Fundamentals of ecology*, 3rd edition. W. B. Saunders, Philadelphia, 574 pp.
- PALACIOS, T. 1989. Microfósiles de pared orgánica del Proterozoico Superior (región central de la península Ibérica). *Memorias del Museo Paleontológico de la Universidad de Zaragoza*, **3** (2), 1–91.
- PEAT, C. J., MUIR, M. D., PLUMB, K. A., MCKIRDY, D. M. and NORVICK, M. S. 1978. Proterozoic microfossils from the Roper Group, Northern Territory, Australia. *BMR Journal of Australian Geology and Geophysics*, **3**, 1–17.
- PJATILETOV, V. G. 1980. Mikrofosilii dashkinskoi svity Eniseickogo kriazha. *Doklady Akademii Nauk SSSR*, **255**, 453–454. [In Russian].
- PREISS, W. V., WALTER, M. R., COATS, R. P. and WELLS, A. T. 1978. Lithological correlations of Adelaidean glaciogenic rocks in parts of the Amadeus, Ngalia, and Georgina Basins. *Bureau of Mineral Resources Journal of Australian Geology and Geophysics*, **3**, 43–53.
- RASCIO, N., CASADORO, G. and ANDREOLI, C. 1979. Ultrastructural features of *Chlorella nana* sp. nov. *Botanica Marina*, **22**, 223–227.
- ROSENBERG, R. 1974. Spatial dispersion of an estuarine benthic faunal community. *Journal of Experimental Marine Biology and Ecology*, **15**, 69–80.
- SCHAU, M. and BECKETT, M. 1986. High-grade metamorphic rocks of northwestern Melville Peninsula, District of Franklin. *Geological Survey of Canada, Paper*, **86-1A**, 667–674.
- SCHERMERHORN, L. J. G. 1974. Late Precambrian mixites: glacial and/or nonglacial?. *American Journal of Science*, **274**, 673–824.

- SCHIEBER, J. 1986. The possible role of benthic microbial mats during the formation of carbonaceous shales in shallow Mid-Proterozoic basins. *Sedimentology*, **33**, 521–536.
- STAPLIN, F. L. 1961. Reef controlled distribution of Devonian microplankton in Alberta. *Palaeontology*, **4**, 392–424.
- VIDAL, G. 1976. Late Precambrian acritarchs from the Eleonore Bay Group and Tillite group in East Greenland. *Gronlands Geologiske Undersogelse, Rapport*, **78**, 1–19.
- 1979. Acritarchs from the Upper Proterozoic and Lower Cambrian of East Greenland. *Gronlands Geologiske Undersogelse, Bulletin*, **134**, 1–40.
- 1981a. Micropaleontology and biostratigraphy of the upper Proterozoic and lower Cambrian sequence in East Finnmark, northern Norway. *Norges Geologiske Undersokelse*, **362**, 1–53.
- 1981b. Aspects of problematic acid-resistant, organic-walled microfossils (acritarchs) in the Upper Proterozoic of the North Atlantic region. *Precambrian Research*, **15**, 9–23.
- 1990. Giant acanthomorph acritarchs from the upper Proterozoic in southern Norway. *Palaeontology*, **33**, 287–298.
- and DAWES, P. R. 1980. Acritarchs from the Proterozoic Thule Group, north-west Greenland. *Gronlands Geologiske Undersogelse, Rapport*, **100**, 24–29.
- and FORD, T. D. 1985. Microbiotas from the late Proterozoic Chuar Group (northern Arizona) and Uinta Mountain Group (Utah) and their chronostratigraphic implications. *Precambrian Research*, **28**, 349–389.
- and KNOLL, A. H. 1983. Proterozoic plankton. *Geological Society of America, Memoir*, **161**, 265–277.
- and NYSTUEN, J. P. 1990. Micropaleontology, depositional environment, and biostratigraphy of the upper Proterozoic Hedmark Group, southern Norway. *American Journal of Science*, **290-A**, 170–211.
- and SIEDLECKA, A. 1983. Planktonic, acid-resistant microfossils from the upper Proterozoic strata of the Barents Sea region of Varanger Peninsula, East Finnmark, northern Norway. *Norges Geologiske Undersokelse*, **382**, 45–79.
- VOLKOVA, N. A. 1981. Akritarkh verkhnego Dokembriia iugovostochnoi Sibiri (Ustkirbinskaia svita). *Biulleten Moskovskogo Obshchestva Ispytatelei Prirody Otdel Geologicheskii*, **56** (4), 66–75. [In Russian].
- WATERBURY, J. B. and STANIER, R. Y. 1978. Patterns of growth and development in pleurocapsalean cyanobacteria. *Microbiological Reviews*, **42**, 2–44.
- WELLS, A. T., FORMAN, D. J., RANFORD, L. C. and COOK, P. J. 1970. Geology of the Amadeus Basin, central Australia. *Bureau of Mineral Resources Geology and Geophysics, Bulletin*, **100**, 1–222.
- YIN, C. 1990. Spinose acritarchs from the Touthantou Formation in the Yangtze Gorges and its geological significance. *Acta Micropalaeontologica Sinica*, **7**, 265–270.
- ZANG, W. L. 1988. Late Proterozoic–Early Cambrian microfossils and biostratigraphy in China and Australia. Unpublished Ph.D. thesis, Australian National University.
- and WALTER, M. R. 1989. Latest Proterozoic plankton from the Amadeus Basin in central Australia. *Nature*, **337**, 642–645.

NICHOLAS J. BUTTERFIELD

Botanical Museum  
Harvard University  
Cambridge,  
Massachusetts 02138, USA

Present address:  
Department of Earth Sciences  
University of Cambridge  
Cambridge CB2 3EQ, UK

FREDERICK W. CHANDLER  
Geological Survey of Canada  
601 Booth Street  
Ottawa,  
Ontario K1A 0E8, Canada

Typescript received 19 August 1991

Revised typescript received 26 February 1992